How to count kangaroos

H. I. McCallum

Department of Zoology, University of Queensland, Queensland 4072

ABSTRACT

The fundamental reason for counting kangaroos is to ensure that harvests are demonstrably sustainable. Given this goal, it is essential that the survey method should be able to detect broad scale trends in population size. Aerial counts will detect trends only if the constant ("correction factor") that relates the number of sightings to actual population size either remains constant, or the way in which it changes depending on environmental conditions is known. Actual counts, and not an index, are essential if harvesting policy is to be proactive, rather than simply reacting to previous changes in population size. It is evident from other papers in this volume that there is a particular problem in estimating appropriate correction factors for grey kangaroos. Several contributors suggested a research programme to produce better correction factors, which would then be used in the future to correct raw sighting data. A better solution may be to use "double sampling", which is a well-established sampling method. Each time an aerial survey is conducted, a subsample of the transects surveyed would be re-surveyed using helicopter counts, which are more accurate, but more expensive. The ratio of the helicopter to fixed-wing counts is then used to produce a survey-specific correction factor. Double sampling is more expensive than fixed-wing surveys alone, so it would be necessary to decrease the intensity of the fixed-wing surveys to allow for the extra cost of the helicopter surveys. The experiments necessary to see whether double sampling is worthwhile are very similar to those that are necessary to develop better correction factors. I suggest that any experiments designed to improve correction factors should also be analysed to investigate the feasibility of using double sampling to estimate kangaroo population size.

WHY COUNT KANGAROOS?

There is never much point in collecting data without thinking about what those data are to be used for. The underlying reason that all Australian mainland States (except Victoria and the Northern Territory) spend considerable resources in counting kangaroos is to ensure that the kangaroo harvest is managed appropriately. So, any discussion of the adequacy of current methods of counting kangaroos must start with a discussion of the objectives of the kangaroo management, and the way in which data on kangaroo populations relate to these management objectives.

The general consensus of the workshop was that the fundamental objective of kangaroo management is to maintain viable populations of all exploited species over their current range, while allowing for both a sustainable and viable kangaroo industry and for reductions in populations where they contribute to overgrazing.

Sustainability of harvests of wild animals is discussed in great detail in the fisheries literature (Hilborn and Walters 1992). However, few of the major exploited fish stocks have been managed sustainably (Beddington and Basson 1994; Hutchings and Myers 1994). The Grand Banks cod fishery was arguably the most important in the world, from a historical and social perspective (Kurlansky 1997). It has now collapsed entirely. We should not be overconfident about our ability to manage

harvests sustainably, particularly when social and political issues are important. There is, however, one very significant difference between managing fish populations and managing populations of large terrestrial vertebrates, such as kangaroos. Most of the data used to monitor fish populations are catch data. They come from the commercial exploitation itself. Many of the problems that have occurred in fisheries management are direct results of the tendency for catch per unit effort to remain high as abundance decreases through overexploitation (Hilborn and Walters 1992). In contrast, the Australian kangaroo harvest is monitored primarily by surveys, independent of the harvest. Independent survey data do not have most of the inherent problems of catch per unit effort data.

I do not propose to discuss sustainability in detail, other than to note that a sustainable harvest is one that does not lead to a continuing decline in the population being exploited, and that sustainable harvests may be at, below, or above, the point of maximum sustainable yield. To my knowledge, no-one has ever suggested that an objective of kangaroo harvesting should be to extract the maximum sustainable yield from the population. A viable harvest is not necessarily the same thing as a sustainable one, although it is obvious that an unsustainable harvest cannot be viable in the long term. Viability means that the harvest must be capable of

economically supporting participants in it. For the specific purposes of this discussion, it is essential to recognize that a viable harvest depends crucially on the existence of continuing markets for kangaroo products. Those markets will be threatened if the harvest cannot be demonstrated to be sustainable, in the face of substantial hostility from certain organizations. The monitoring system must not only ensure that the harvest is sustainable, it must ensure that the harvest is seen to be sustainable.

There is no general consensus about the extent to which kangaroos actually do contribute to overgrazing, with the consequences to either land degradation or competition with livestock. This is an important debate, but is beyond the scope of this article, and was not considered in detail at the workshop. Most primary producers believe that kangaroo populations do need to be reduced, at least some of the time, to prevent overgrazing. They are supported in this belief by most state departments responsible for primary industries, and by some biologists outside such departments (Wilson et al. 1984; Freudenberger et al. 1997). However, other biologists, particularly those who have undertaken controlled experiments, doubt that overgrazing by kangaroos is often a significant land management issue. For example, Edwards et al. (1996) suggested that competition between sheep and kangaroos rarely occurred. Whatever the actual reality, the political reality is that kangaroo shooting 'pest reduction" purposes will continue for the foreseeable future in most Australian States. An objective of kangaroo monitoring is therefore to ensure that such "pest reduction" is consistent with the overall objective of maintaining kangaroo populations as viable across their range. To determine whether kangaroo populations are at a level such that they do cause land degradation is not a major objective of current monitoring schemes, although South Australia is moving in this direction (Alexander 1997). It cannot become a central objective until the relationship between kangaroo grazing and land degradation is better established.

AN INDEX OR AN ESTIMATE OF ABUNDANCE?

An important issue, discussed at some length in the workshop, is whether it is essential to produce an estimate of the actual number of kangaroos, or whether an index of abundance is adequate. It is often assumed that an index is an easier quantity to obtain and work with than an actual population estimate. As has been pointed out a number of times (e.g.,

Pollock 1995), the use of an index relies on an implicit assumption that

$$N = \alpha I \tag{1}$$

where N is the actual population size, I is the index, and α is a constant of proportionality connecting the index to the actual population size.

There are two implicit assumptions in eqn (1). First, there is the assumption of direct proportionality. If there is a curvilinear relationship between the index and population size, or if there is a non-zero intercept, the index cannot be used to compare relative density through space or time. However, if the nonlinear relationship between the index and actual population size can be described, the index can be still be converted into an estimate of population size. Cairns (1999) provided evidence that the problem of nonlinearity is not a major one if aerial sightings are used as an index of kangaroo population.

The second, and more serious, implicit assumption is that the constant a is indeed constant, both through time and across space. This assumption is impossible to test if only the index \hat{I} is available. If it can be tested and verified against the true population size, there is no need to use the index anyway, as eqn (1) could then be used to obtain an estimate of actual population size. In some cases, this second assumption can be circumvented by estimating a series of constants. Each might be appropriate for a particular habitat or season, or some combination of both. To estimate these constants, or "correction factors", it would be necessary to have a series of index values and actual counts in various habitats, seasons etc.

Whenever an index is used alone, instead of being converted to an actual estimate, what is being asserted is that, while the constant is unknown, it is known to be constant. This is a difficult assertion to maintain. In the context of kangaroo counting, the index is typically an uncorrected aerial count, and the constant is the "correction factor". For red kangaroos, there is good evidence that correction factors do not change markedly through time (Pople 1999). The 20 years of red kangaroo survey data from South Australia (Grigg et al. 1999) are therefore a regular and consistent record of the dynamics of a large, wild herbivore over a spatial scale and length of time that is probably unique. The only comparable data are for caribou in the Arctic (Caughley and Gunn 1993), or possibly for wildebeest in Africa (Campbell and Borner 1995), although neither of these

covers the spatial scale and has the regularity of the red kangaroo data.

Assuming that α is constant through time and space (something I will discuss later), the question that then can be asked is whether it is necessary to know its value. If we have convinced ourselves (and hopefully others) that aerial counts are directly proportional to kangaroo abundance, do we really need to know what the constant of proportionality is? Given that a sustainable harvest is one that does not lead to a continuing decline in kangaroo numbers, an index that does not decline through time demonstrates that the previous harvests have been sustainable. One could go further and suggest that if current harvests are set on the same policy as before, then an index that maintains its value through time gives confidence that current harvests are sustainable too. The difficulty is that kangaroo populations vary greatly through time, largely due to the influence of rainfall, but the periods of increase and decrease generated by rainfall variation may be many years long (Caughley 1987a; Grigg et al. 1999). This means that evidence that a harvest level (whether defined as effort, numbers or proportion) is not sustainable may not be clear for a number of years. Any setting of harvest levels only with respect to an index therefore operates with a substantial lag.

Currently, kangaroo harvest levels are approved by the Commonwealth as quotas: actual numbers that may be taken in a given year. Quotas are currently set and justified as proportions of the total population. This is because determining the impact that a given quota will have on a population is a matter of determining the per capita level of mortality that the quota is equivalent to. This requires an estimate of the actual population size, not simply an index, connected to the population size by some unknown constant. Without an absolute population estimate, any harvest policy can only be reactive, rather than pro-active. It may be possible to measure the impact that a harvest with a given quota has had on a population, but not to predict what effect it will have on a population, except to conjecture that it may be similar to the effect of a previous quota of similar size in the past. It will also be difficult to defend publicly a quota based purely on an index.

HOW KANGAROOS ARE COUNTED CURRENTLY

Population size of animals can be estimated in a number of ways, including mark-recapture methods, visual counts and a variety of indirect methods (see Seber 1982 for a review). Although mark-recapture or resight methods have been successful in estimating the local abundance of smaller macropods, there is little doubt that only direct visual counts are able to be used to estimate the abundance of the larger macropods over the spatial scales necessary to set harvest policies. It is also generally accepted that, of all current visual census methods, line transects carried out on foot produce estimates that are closest to actual kangaroo abundance (Southwell 1994). While they are valuable to calibrate other methods, foot transects are not possible at the large scales of state-wide surveys. States therefore base their population estimates on aerial surveys.

Queensland currently uses annual helicopter surveys using line transect methods (Lundie-Jenkins et al. 1999). A line transect (Buckland et al. 1993) uses the frequency distribution of distances of sighted individuals from the transect line to estimate abundance. All individuals on the line are assumed to be seen, but the method assumes that some animals away from the line will be missed. A strip transect, in contrast, simply counts all individuals seen within a certain distance of the line). Evidence from Queensland research (Clancy et al. 1997) suggests that helicopter surveys record similar population densities to walked transects, for red and eastern grey kangaroos, but still undercount wallaroos (euros). Helicopter surveys are expensive, although it may be that ultralight aircraft can be used to produce similar results for less cost (Grigg et al. 1997). The expense and short range of helicopters means that Queensland monitors populations on several fixed monitor blocks only (Lundie-Jenkins et al. 1999), rather than extensively across the entire state.

The remaining states count kangaroos using strip transects surveyed from fixed-wing aircraft. New South Wales and South Australia use extensive annual surveys with two (New South Wales) or four (South Australia) transect lines being flown per degree square throughout the main harvest area (Grigg et al. 1999; Gilroy 1999), covering a large part of the kangaroo range within each state. Western Australia uses similar extensive surveys, but on a less frequent basis. All three states adjust the actual numbers seen to produce an estimated actual population, using correction factors originally derived by Graeme Caughley for red kangaroos (Caughley et al. 1976). There is consensus that the correction factors for red kangaroos return reasonable estimates, but that grey kangaroo and wallaroo populations are grossly underestimated.

SIGHTABILITY OF KANGAROOS FROM THE AIR

All kangaroos present on the ground will not be seen from the air, particularly in a fixed-wing survey. To translate an aerial count into an estimated population size, it is necessary to estimate the sightability, which is the probability of seeing an animal, given that it is present within the area being counted. As Pople (1999) pointed out, visibility is a function of species, behaviour, habitat and observer. The likelihood is that it also depends on interactions between these factors, rather than simply being able to be estimated as a multiple of individual probabilities for each of the above factors.

In ground counts and helicopter surveys using line transect methods, the distance to the sighted individual or group is recorded. Provided all animals actually on the transect line (i.e., zero distance) are seen, the use of appropriate software (Laake et al. 1993) enables these counts to be corrected for sightability. Strip transect methods, however, require sightability to be estimated from information additional to that provided by the survey itself.

To improve the accuracy of fixed-wing aerial counts, three things can be done with sightability. It can be improved, to increase the mean value of the raw count. It can be standardized, to reduce the variation in counts between replicate aerial transects. Finally, if it can be estimated, it can be used to correct the raw sighting index, and translate it into an actual estimate. Improving mean sightability and reducing its variation (or coefficient of variation) are issues that cannot be discussed separately. Some measures may improve both, whereas others may trade one off against the other. Few ways of improving mean sightability have no consequences for its coefficient of variation.

First, there is the possibility of reducing the strip width over which kangaroos are counted from the current 200 m to 100 m. This is likely to increase the probability of an animal on the strip being sighted, as the search pattern of the observers can be concentrated, and there will no longer be attempts to count animals away from the track of the aircraft. On the other hand, fewer animals will be on a strip of half the width, and it is likely that fewer will be counted for the same expense and effort. All other things being equal, the larger the total number of individual animals counted in a survey, the lower will be the resulting standard error in the final estimated density. There is an optimum strip width for any visual survey, and experiments to ensure that 100 m is not closer to this optimum than 200 m are warranted. Stuart Cairns (University of New England) and Josh Gilroy (NSW National Parks and Wildlife Service) will undertake a large-scale experimental programme to address this issue, among others.

A related suggestion to increase the sightability of kangaroos on the transect being surveyed, at the cost of surveying less area for the same flight time, is to count from one side of the aircraft only. It is clear that "away from the sun" counting is much easier than "towards the sun" counting. Using only one observer to count away from the sun would reduce personnel requirements considerably, and possibly increase the reliability of the counts, but it would also reduce the total area surveyed.

Observer training is a crucial issue in both increasing the mean sightability and reducing its coefficient of variation. Beard (1999) produced data showing that the number of kangaroos seen by a trainee observer, relative to that seen by a trained observer, does not reach an asymptote until after at least 10 flights. Similarly, the number of kangaroos seen per transect by a trainee is much more variable than that counted by an experienced observer. Some observers, despite experience with kangaroos, do not seem to approach the sighting levels of experienced observers at all. Clearly, there is a major problem in setting fixed "correction factors" unless all observers have been calibrated against a single "experienced observer" standard. Such a standard probably does not exist, as even experienced observers differ in the mean number of kangaroos that they will see on the same transect.

STRATIFICATION

One way to produce major improvements in the precision of overall estimates of kangaroo density is to use stratified sampling methods. The idea is extremely simple. If some mappable characteristic of the environment is thought to influence kangaroo density, then the total area for which the estimate is required is divided into a small number of separate subareas (or strata) on the basis of this characteristic. The population density, and its standard error, is then estimated separately for each stratum, and the results are combined to give an overall estimate. Strata should be selected so that variation between them in density is maximized, with the consequence that variation within them is minimized. The obvious mappable characteristic to use in this particular situation would

be vegetation type. Precision is maximized if sampling effort is allocated between strata proportional to the overall kangaroo population in each stratum, but substantial gains in precision are possible if sampling is random or systematic across the entire study area, or even if stratification is done after sampling is completed.

THE PROBLEM WITH GREY KANGAROOS

The biggest problems with aerial strip transects occur when counting grey kangaroos (both eastern and western). There are similar difficulties with wallaroos, but as the commercial harvest of this species is relatively small, the implications are not as serious. There was total consensus among workshop participants that the correction factors originally derived by Graeme Caughley grossly undercount greys, and that they need to be at least doubled. Some participants suggested quadrupling them was more appropriate. Whatever the most appropriate correction factor is, such ad hoc doubling and re-doubling is better suited to a poker game than to the management of a major wildlife harvest.

Sightability of grey kangaroos is much lower than that for reds primarily because they prefer less open habitats than do reds, and are therefore more likely to be hidden from an aerial observer. Several participants in the workshop suggested that the solution to the correction factor problem for grey kangaroos is to undertake a substantial research programme to establish improved correction factors. The idea would be to survey grey kangaroos in a variety of habitats, using both aerial strip counts and helicopter counts. Assuming that the helicopter counts are close to being complete counts, an improved set of correction factors would be developed. This would represent a considerable improvement over the current situation.

I have several misgivings about this as a complete solution to the problem. First, "open" or "closed" habitats may be quite different things in terms of vegetation structure or composition across the range of grey kangaroos. Even if objective definitions in terms of percentage tree cover were developed, the grain or patchiness in the habitat will vary considerably, as will the tree species making up the canopy. Such factors may well influence sightability considerably. It would certainly be possible to test whether this problem is substantial, but the costs would be considerable. Realistically, the likelihood is that factors established in one part of the country would be applied uncritically in others. Second, it is well known that kangaroos have different habitat preferences in different environmental conditions (Caughley 1987b; Hill et al. 1987; Pople 1989; Southwell 1989). If such habitat shifts occur at a large scale, then habitat-dependent correction factors may allow for consistent estimation of population size in different environmental conditions. However, correction factors would necessarily be applied at the transect scale, of several kilometres. If habitat selection occurs at the fine scale of patches within transects, then habitat-specific correction factors would not assist. Third, drought is likely to change sightability within particular habitat types. Fourth, a fixed set of correction factors does not allow for differences between observers. Finally, the problem with a single set of correction factors is that they are likely to become fixed in usage, and not reviewed until their faults are gross. The experience with the original correction factors derived by Graeme Caughley epitomizes this last point.

Is there an alternative to fixed correction factors?

IS DOUBLE SAMPLING A SOLUTION?

A method known as double sampling offers an alternative to the use of fixed correction factors. The basic idea would be to survey a large number of transects using fixedwing aerial survey methods, and then to use a more intensive and accurate sampling method (such as helicopter surveys) to obtain a more accurate estimate on a subsample of those transects. The ratio of helicopter counts to fixed-wing counts is estimated from the subsample, and used to correct the counts on the full sample. Details of the method are in standard textbooks on sampling strategies (e.g., Thompson 1992) and it is widely used in wildlife surveys in North America (Prenszlow and Lovvorn 1996).

There are two major advantages in using double sampling compared with fixed correction factors. First, because the correction is recalculated in each survey, changes in average sightability that occur through time are allowed for. This is the case whether they occur because of changes in actual visibility in a given habitat, habitat shift, or inter-observer variability. Second, the estimated error in the final estimate incorporates a component due to the error in the estimation of the correction factor. This means that the precision of the final estimate is better described than it is by applying a fixed correction factor. The error in an estimate based on a fixed correction factor is underestimated, as well as the estimate itself being biased in an unknown fashion.

There is an obvious disadvantage in double sampling: cost. To add an expensive, but accurate estimation method on top of the current intensity of fixed-wing aerial surveys will considerably increase the total cost of kangaroo surveys. The suggestion should not necessarily be that the resources dedicated to kangaroo surveys should be increased to allow for double sampling. It may be that the existing resources would be better allocated by reducing the intensity of fixed-wing aerial survey to allow for some double sampling.

EXTENSIVE VERSUS INTENSIVE SURVEYS

The current fixed-wing aerial surveys are expensive. Despite this cost, all participants in the workshop agreed that the estimates of grey kangaroo numbers produced may be out by a factor of at least two. This is not a satisfactory state of affairs. It is almost certainly the case that the surveys may detect changes in grey kangaroo numbers with far greater accuracy than they estimate actual numbers, but this relies on the assumption that the uncorrected counts are an adequate index of grey kangaroo population size. As I discuss above, if only changes in numbers are estimated, harvest management becomes reactive, and cannot be proactive.

It is certainly worth exploring the possibility of changing the basis of the surveys. The current design in all states except Queensland attempts a complete geographical coverage of the main kangaroo populations, but uses a method that is known to be inaccurate for grey kangaroos. The alternative is to use a more accurate estimation process, carried out over an appropriately selected sample from the total geographic area. This is essentially the approach Queensland currently takes, using helicopter surveys over selected monitor blocks (Lundie-Jenkins et al. 1999). Whether the 10 Queensland monitor blocks can really be considered an appropriate sample from the total area of kangaroo distribution is doubtful. They bear some resemblance to a stratified sample, as there is some replication within each of the major biogeographic zones of the state within which kangaroos are common. These biogeographic zones could be considered as strata. Clancy (1999) discussed the advantages and disadvantages of the Queensland approach relative to the approach of the other states.

A double sampling approach offers the prospect of combining some of the best features of both helicopter and fixed-wing surveys, while placing the whole procedure in a more secure theoretical framework. I would see the broad design as operating as follows:

- 1. Identify a small number of major zones within the state that are geographically contiguous, and across which kangaroo populations can be expected to vary, in species composition or density. These are the basic strata.
- 2. Within strata, identify (preferably at random) a small number (5-10) of blocks, or strips, within which kangaroo populations are to be monitored. Fixed-wing transects would then be flown across these areas. These are then cluster samples.
- 3. A subsample of the fixed-wing transects within each block is then selected for helicopter or ground sampling. This is the double sampling step.

For this approach to be feasible financially, it is clear that the total number of strip transects would need to be fewer than the current number. It should be possible to model the alternative strategies, including costs and reasonable assumptions about kangaroo distributions, to see if the alternative approach is feasible.

A decision that must be taken is whether the blocks and transects should be kept fixed, or re-randomized each year. A general rule is that fixed sampling units are better able to detect changes through time, but rerandomized sampling units will better estimate population size at any given time.

A problem with the above proposal is that the optimal sample allocations to monitor grey and red kangaroos will be different. Some sort of compromise would need to be established, but there would still be major gains in precision compared with a random allocation.

WHERE TO FROM HERE?

To immediately replace the current monitoring system with double sampling would be premature. It is necessary to first demonstrate that, for the same cost, double sampling will lead to better estimates of kangaroo population size than provided by the current fixed-wing surveys. The previous discussion merely suggests that it may. Much of the information necessary to make an informed decision is already available. The records of aerial surveys across extensive areas of New South Wales and South Australia for a number of years form a database that can easily be subsampled to simulate stratified surveys from only a sample of areas. Subsampling would result in some loss of precision

in the estimate of the uncorrected mean number of sightings per unit area, as fewer individual transects would be used in the estimate. Simulation could explore the extent that the standard error in the mean uncorrected index increased, and more importantly, whether the same trends that are observed in the extensive counts can be consistently picked up in subsamples. It would not be difficult to cost subsamples in various locations across a state, including personnel, flight survey time and ferry time.

The element of double sampling that cannot easily be investigated using currently available data is the strength of correlation between fixed-wing and helicopter counts in different locations and at different times. If this correlation is very strong and consistent, then double sampling is unnecessary. All that is needed is a single set of correction factors calculated once, and precision would be maximized in the future by directing all available resources to fixed-wing surveys. On the other hand, if the correlation were entirely absent, then fixed-wing surveys would be useless, and all resources should be dedicated to helicopter surveys. Based on evidence from Queensland (Clancy et al. 1997; Pople et al. 1998a,b), the real answer lies somewhere in between: there is a good, but imperfect correlation between fixed-wing and helicopter counts, and both the strength of the relationship and its regression coefficient vary somewhat through space and time. If this is the case, then the best sampling strategy is double sampling, with the optimal allocation of effort between fixed-wing and helicopter surveys depending both on the strength of the correlation between the two and their relative costs.

Fortunately, the experiments necessary to determine the optimal allocation of effort for double sampling are very similar to those needed to produce improved correction factors. Essentially, what is needed for either purpose is a series of counts on the same transects, repeated both using fixed-wing and helicopter surveys. For either purpose, these surveys would need to be carried out in a variety of habitats and geographical locations, and for a variety of kangaroo densities. My proposal, therefore, is that any experiments designed to produce improved correction factors be so designed that they also act as a pilot double sampling survey.

ACKNOWLEDGEMENTS

I would like to thank Gordon Grigg and Tony Pople for comments on an earlier draft of this manuscript.

REFERENCES

- Alexander, P., 1997. Kangaroo culling, harvesting and farming in South Australia — an ecological approach. Aust. Biol. 10: 23-29.
- Beard, L. A., 1999. Training observers. Aust. Zool. 31: 287-91.
- Beddington, J. R. and Basson, M., 1994. The limits to exploitation on land and sea. *Phil. Trans. R. Soc. Lond. B* 343: 87-92.
- Buckland, S. T., Anderson, D. R., Burnham, K. P. and Laake, J. L., 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall: London.
- Campbell, K. and Borner, M., 1995. Population trends and distribution of Serengeti herbivores: implications for management. Pp. 117-45 in Serengeti II: dynamics, management and conservation of an ecosystem ed by A. R. E. Sinclair and P. Arcese. University of Chicago Press: Chicago.
- Caughley, G. and Gunn, A., 1993. Dynamics of large herbivores in deserts: kangaroos and caribou. *Oikos* 67: 47-55.
- Caughley, G. C., 1987b. The effect of drought on kangaroo populations: a response. J. Wildl. Manage. 51: 603-04.
- Cairns, S. C., 1999. Accuracy and consistency in the aerial survey of kangaroos. Aust. Zool. 31: 275-79.
- Caughley, G., 1987a. Ecological relationships. Pp. 159-87 in Kangaroos: their Ecology and Management in the Sheep Rangelands of Australia ed by G. Caughley, N. Shepherd and J. Short. Cambridge University Press: Cambridge.
- Caughley, G., Sinclair, R. and Scott-Kemmis, D., 1976. Experiments in aerial survey. J. Wildl. Manage. 40: 290-300.
- Clancy, T. F., 1999. Choice of survey platforms and technique for broad-scale monitoring of kangaroo populations. *Aust. Zool.* 31: 267-74.
- Clancy, T. F., Pople, A. R. and Gibson, L. A., 1997. Comparison of helicopter line transects with walked line transects for estimating densities of kangaroos. *Wildl. Res.* 24: 397-409.
- Edwards, G. P., Croft, D. B. and Dawson, T. J., 1996. Competition between red kangaroos (*Macropus rufus*) and sheep (*Ovis aries*) in the arid rangelands of Australia. *Aust. J. Ecol.* 21: 165-72.
- Freudenberger, D., Noble, J. and Hodgkinson, K., 1997.
 Management for production and conservation goals in rangelands. Pp. 93-106 in Landscape Ecology, Function and Management: Principles from Australia's Rangelands ed by J. Ludwig, D. Tongway, D. Freudenberger, J. Noble and K. Hodgkinson. CSIRO Publishing: Collingwood.
- Gilroy, J., 1999. Kangaroo monitoring in relation to kangaroo management in New South Wales. Aust. Zool. 31: 306-08.
- Grigg, G. C., Pople, A. R. and Beard, L. A., 1997. Application of an ultralight aircraft to aerial survey of kangaroos on grazing properties. *Wildl. Res.* 24: 359-72.
- Grigg, G. C., Beard, L. A., Alexander, P., Pople, A. R. and Cairns, S. C., 1999. Aerial survey of kangaroos in South Australia 1978-1998: a brief report focusing on methodology. Aust. Zool. 31: 292-300.

- Hilborn, R. and Walters, C. J., 1992. Quantitative fisheries stock assessment: choice dynamics and uncertainty. Chapman and Hall: New York.
- Hill, G. J. E., Barnes, A. and Wilson, G. R., 1987. The effect of drought on kangaroo populations: a comment. J. Wildl. Manage. 51: 602-03.
- Hutchings, J. A. and Myers, R. A., 1994. What Can Be Learned from the Collapse of a Renewable Resource? Atlantic Cod, Gadus morhua, of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. 51: 2126-146.
- Kurlansky, M., 1997. Cod. A biography of the fish that changed the world. Johnsthon Cape: London.
- Laake, J. L., Buckland, S. T., Anderson, D. R. and Burnham, K. P., 1993. DISTANCE User's Guide V2.0. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University: Fort Collins, CO. (http://www.ruwpa.st-and.ac.uk/distance)
- Lundie-Jenkins, G., Hoolihan, D. W. and Maag, G. W., 1999. An overview of the Queensland macropod monitoring programme. Aust. Zool. 31: 301-05.
- Pollock, K. H., 1995. The challenges of measuring change in wildlife populations: a biometrician's perspective. Pp. 117-21 in Conservation Through the Sustainable Use of Wildlife ed by G. C. Grigg, P. T. Hale and D. Lunney. Centre for Conservation Biology, University of Queensland: Brisbane.
- Pople, A., 1989. Habitat associations of Australian Macropodoidea. Pp. 755-66 in Kangaroos, Wallabies and Rat-kangaroos, Vol. 2 ed by G. Grigg, P. Jarman and I. Hume. Surrey Beatty & Sons: Chipping Norton, Sydney.
- Pople, A. R., 1999. Repeatability of aerial surveys. Aust. Zool. 31: 280-86.

- Pople, A. R., Cairns, S. C., Clancy, T. F., Grigg, G. C., Beard, L. A. and Southwell, C. J., 1998a. An assessment of the accuracy of kangaroo surveys using fixed-wing aircraft. Wildl. Res. 25: 315-26.
- Pople, A. R., Cairns, S. C., Clancy, T. F., Grigg, G. C., Beard, L. A. and Southwell, C. J., 1998b. Comparison of surveys of kangaroos in Queensland using helicopters and fixed-wing aircraft. Rangel. J. 20: 92-103.
- Prenszlow, D. M. and Lovvorn, J. R., 1996. Evaluation of visibility correction factors for waterfowl surveys in Wyoming. J. Wildl. Manage. 60: 286-97.
- Seber, G. A. F., 1982. The estimation of animal abundance and related parameters, 2nd ed. Griffin: London.
- Southwell, C., 1989. Techniques for monitoring the abundance of kangaroo and wallaby populations. Pp. 659-93 in Kangaroos, Wallabies and Rat-kangaroos, Vol. 2 ed by G. Grigg, P. Jarman and I. Hume. Surrey Beatty & Sons: Chipping Norton, Sydney.
- Southwell, C., 1994. Evaluation of walked line transect counts for estimating macropod density. J. Wildl. Manage. 58: 348-56.
- Thompson, S. K., 1992. Sampling. Wiley-Interscience: New York.
- Wilson, A. D., Harrington, G. N. and Beale, I. F., 1984. Grazing management. Pp. 129-39 in Management of Australia's Rangelands ed by G. N. Harrington, A. D. Wilson and M. D. Young. CSIRO Publications: East Melbourne.